

**Studies on the Biology of *Heliconius charitonius* L.
in Costa Rica**

(Nymphalidae: Heliconiinae)

ALLEN M. YOUNG

*Division of Invertebrate Zoology, Milwaukee Public Museum,
Milwaukee, Wisconsin 53233*

The heliconiine butterfly *Heliconius charitonius* L. (Nymphalidae), is one of the most geographically widespread members of this subfamily (Heliconiinae) throughout tropical America (e.g., Comstock and Brown, 1950; Brown and Comstock, 1952). The adult is strikingly different in appearance from many other sympatric heliconiines by the distinct black and yellow color pattern of the wings. Adults of this species are known to roost communally (Jones, 1930; Poulton, 1931; Young and Thomason, 1975), a sophisticated behavioral trait (Gilbert, 1975) it shares with other *Heliconius*. Although the early stages of various *Heliconius* have been studied in Trinidad (Beebe, Crane, and Fleming, 1960; Alexander, 1961a, b) and Brazil (e.g. Brown and Mielke, 1972), little is known about the biology of *H. charitonius* in Central America. The apparent coevolutionary associations of *Heliconius* with certain plant groups in the tropics (Benson *et al.*, 1975; Gilbert, 1975) warrants the study of selected species. This paper summarizes studies on the adult and juvenile biology of *H. charitonius* in Costa Rica.

STUDY AREA AND METHODS

Heliconius charitonius was studied near La Virgen de Sarapiquí (Heredia Province) in northeastern Costa Rica; adults and early stages were observed or collected from a strip of young secondary forest (5 years old) bordering a dirt road that separates Finca La Tigre (property of Compañía Agrícola Myristica, S.A.) and Finca de Oscar Arias. This region of Costa Rica is a transitional zone between premontane and lowland tropical wet forest; it is about 200 meters in elevation with a short, erratic dry period during March and April. Although the area includes primary wet forest habitat, much of it has been converted to various successional stages of secondary forest and cultivated land.

Both field and laboratory studies on *H. charitonius* were carried out from January 11 to February 15, 1976. During this period, field observations were conducted as follows: January 11–12 (2 days), January 15–17 (3 days), January 26–30 (5 days), February 4–7 (4 days), and February 11–15 (5 days). Field studies consisted of (1) searches

for early stages, (2) observations on oviposition behavior, (3) observations on the mortality of early stages, (4) recording of adult feeding sites, and (5) recording of other heliconiines active in the same habitat. Laboratory studies dealt with the rearing of individuals from the egg stage primarily for the description of the life cycle, and the estimation of developmental time. Individuals were reared by confining eggs and fresh clippings of the larval host plant into a clear plastic bag kept tightly shut. Field observations were made at several different times during the day.

RESULTS

Habitat, Oviposition, and Larval Host Plant.—*Heliconius charitonius* occurs primarily in young secondary forest tropical communities, where adults visit various inflorescences throughout sunny hours of the day. The primary flowers visited include several Compositae, one or more species of Curcubitaceae and *Cephaelis tomentosa* (Rubiaceae). The Compositae visited have either white or yellow inflorescences while the other plant families visited have deep orange or red inflorescences. It is very likely that adults feed on pollen (Gilbert, 1975), although "pollen loads" on probosci are less frequently encountered in this species relative to other microsympatric species such as *H. hecale*, which bears notoriously large pollen loads. Gilbert (1972), however, reports heavy pollen loads for *H. charitonius*. Adults generally visit flowers throughout the day on clear sunny days.

Typical flower visitations by *H. charitonius* relative to other *Heliconius* species, occurred on the sunny morning of February 13, 1976. In a forest edge clearing where one curcubit species and *Cephaelis tomentosa* were in bloom, with their patches separated by only four meters of bare ground, *H. charitonius* visited both. There were seven flowers of *C. tomentosa* with full inflorescences (although 35 in total were present, most of these had dropped the yellow corolla tubes), and eleven flowers of the curcubit. One "fresh" adult visited a curcubit flower at 9:05 A.M. and a "worn" adult soon followed suit at 9:15 A.M. This same individual then flew across and visited a *Cephaelis* flower by 9:18 A.M. Since no butterflies were marked, "trapping" or other movement patterns could not be demonstrated. Two other species active in this area visited both flowers: at least two different adults of *H. hecale* ("fresh"; "worn") together gave a total of four visits to curcubit flowers and three visits to *Cephaelis*, while at least two adults of *H. cydno* ("fresh"; "worn") were scored twice on *Cephaelis* and four times on the curcubit. All of these visits occurred between 8:40 and 9:55 A.M. A similar pattern of visits for the same three species was seen the following



FIG. 1. Egg positioning and the egg stage of *Heliconius charitonius*. Upper left: three eggs are shown in a folded terminal bud of leaflets of *T. lobata*. Upper right: three eggs are shown; note one egg adjacent to a young extrafloral nectary. Lower left: top view of one egg nestled down in folded leaflets; lower right: the egg.

morning. Both *H. hecale* and *H. cydno* are more frequent visitors at these particular flowers than *H. charitonius*.

Adults are concentrated in large numbers on a daily basis in patches of young secondary forest where the primary larval host plant, *Tetrastylis lobata* (Passifloraceae) is found in close proximity to adult feeding sites. *Tetrastylis lobata* is the primary plant used for oviposition by

H. charitonius in this region of Costa Rica, despite the fact that it often occurs together with other passifloraceous vines such as *P. vitifolia* and *P. edulis*. Adult vines of *T. lobata* are very large and consist of large, bulky patches growing over other vegetation. It generally flowers during January and February, and *H. charitonius* lays eggs on young and adult vines.

Although eggs are laid singly, a female may lay several eggs on the yet folded terminal leaf buds of *T. lobata* (Fig. 1). One female laid five eggs on a single terminal leaf bud within a 20-minute period one morning. I observed a total of four ovipositions; the first occurred on January 11, 1976 (3:00 P.M.). The female in this instance was very worn and tattered, and she took about 20 seconds to lay one egg. During the oviposition, the wings were fluttering at a steep angle to the body. Several other individuals of *H. charitonius* were flying in the immediate vicinity of this female, but this did not stop the oviposition. On another day (January 16), a female (fresh) laid three eggs in quick succession on a single terminal unit of folded leaf buds. I have also observed that different females very likely lay their eggs on the same unfolded leaf units or that the same female will return to lay eggs on the same leaf unit on different days. Individual females, presumably searching for oviposition sites, spend a great deal of time selecting such sites. Sometimes the egg is nestled far down into the whorl of folded leaves, making only the apical aspect visible (Fig. 1). In addition to eggs being attached to folded leaf buds, they may also be found on the stem near the leaf bud (Fig. 1). Oviposition on tendrils has not been observed. On large vines, eggs are often laid near the top, where most of the folded leaf buds are found; on young vines, eggs are often laid within a few centimeters of the ground, and amidst tall grasses that cover them. As with feeding, I have observed oviposition throughout the day in good weather. Although several other heliconiines lay eggs on *Passiflora* in the area, none of these lays eggs on *T. lobata*, and *H. charitonius* does not lay eggs on *Passiflora*. I searched a total of eight vines of *P. vitifolia* and did not find any eggs or caterpillars of *H. charitonius*; I did, however, find caterpillars of *erato*, *cydno* and *hecale*. It is noteworthy that at least six other heliconiines occur in the same habitat: *Agraulis vanillae*, *Philaethria dido*, *Heliconius cydno*, *H. hecale*, *H. erato*, and *H. sara*. All heliconiine eggs found on *T. lobata* here and reared (a total of 15 eggs collected) proved to be *H. charitonius*. Caterpillars of *H. charitonius* feed on both young and old leaves of *T. lobata*.

The following observations on the early stages were made from individuals obtained from a set of eight eggs discovered in a single unit of

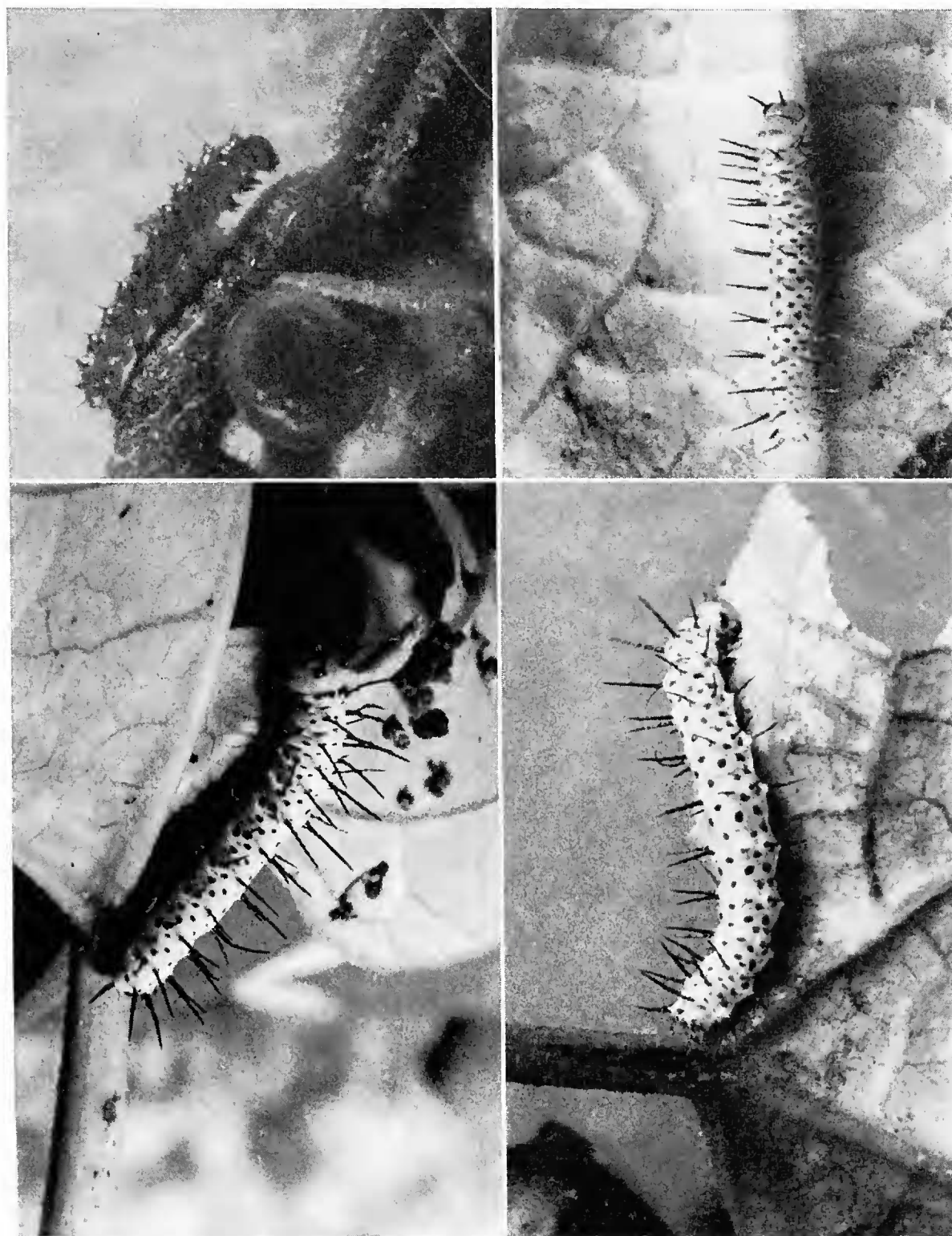


FIG. 2. Caterpillars of *Heliconius charitonius*. Upper left: first instar just above a young extrafloral nectary; upper right: third instar. Lower left: fourth instar; lower right: fifth instar.

folded leaf buds; of the eight eggs, four were reared successfully to the adult stage in the laboratory.

“Disappearances” of Eggs.—Although several eggs were collected for laboratory rearing studies, I left a total of seven additional eggs on vines in the field to see if they hatched successfully. These eggs were on three

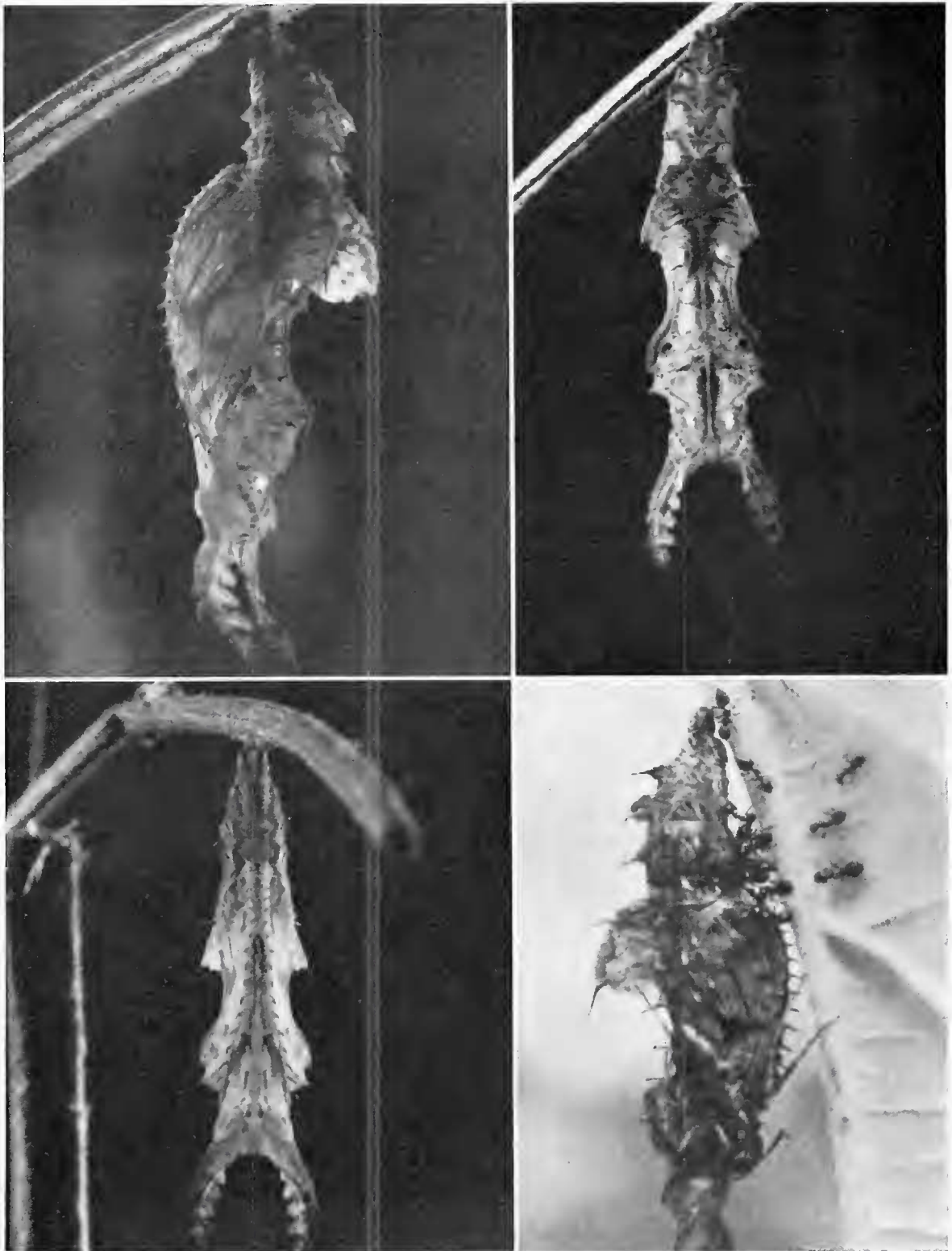


FIG. 3. The pupa of *Heliconius charitonius*. Upper two and lower left photographs: lateral, ventral, and dorsal views respectively. Lower right: a pupa in the field being attacked and eaten by *Crematogaster* ants. Several individuals of a small ant are shown on and along the abdominal region of the pupa; a single individual of a larger ant (*Ectatomma*) is present on the pupa along the frontal area of the wing case (barely in focus).

different vines of *T. lobata*. They all appeared about the same age from their color. Within two days, all were gone, and no first instar larvae were found. I had searched a total of 12 different vines for *Heliconius* eggs, but found only three with eggs in the same area of habitat.

Early Stages.—The large, yellow egg (Fig. 1) is 1.4 mm high and 0.9 mm at the base; it is elongated and truncated at the top and bottom. It lasts five days as measured on four eggs kept in the laboratory.

The first instar larva (Fig. 2) is 3–4 mm at hatching; it is light, translucent orange with a glossy orange-yellow head capsule. It lasts two days (as measured on four individuals).

The second instar bears the full complement of head and body scoli, with the ground color of the body remaining light orange. The scoli are black and branched. The head scolus is about 1.2 times the head height. The dorsal prothoracic plate or crest is thin. This instar lasts four days and attains a length of 7 mm.

The third, fourth, and fifth instars are virtually identical in appearance (Fig. 2). The basic color of the body is bluish-white and the head capsule is a glossy pale lemon-yellow. All scoli are black. The head capsule possesses two sets of black blotches. All legs are dull orange; the anal clasper is dull orange with a black spot dorsally. The dark spots on the body segments (Fig. 2) are very dark reddish-brown. The head scolus is about one-half the height of the head. The third instar lasts four days and reaches a length of 13 mm; the fourth instar lasts four days and reaches 30 mm, and the fifth instar lasts three days and reaches 41 mm. A pinkish prepupa (30 mm long) is active prior to pupation.

The highly sculptured pupa (Fig. 3) is about 30 mm long with the basic color being brownish-orange. It is moderately patterned with dark lines and reflective silver spots. The silver spots are paired and situated dorsally in the thoracic region and first abdominal segment. Fine streaks of white occur on the wing cases. The head bears broad, well developed spatulate appendages that are 5 mm long. Dorso-lateral flanges occur on the third and fourth abdominal segments (smaller on the fourth) and bearing long, outward and downward-directed spines; shorter spines occur on the fifth, sixth, and seventh segments. Short spines with tubercles as bases occur on the metathorax and also on the first and second abdominal segments. Very short spines occur along the antenna cases (at forewing costal sutures); there are very slight tubercles on the wing cases in future cells M_3 - Cu_1 and Cu_1 - Cu_2 . As measured on four individuals, the pupa lasts 10 days for both sexes. From four pupae two males and two females were obtained; three of these adults are shown in Fig. 4.

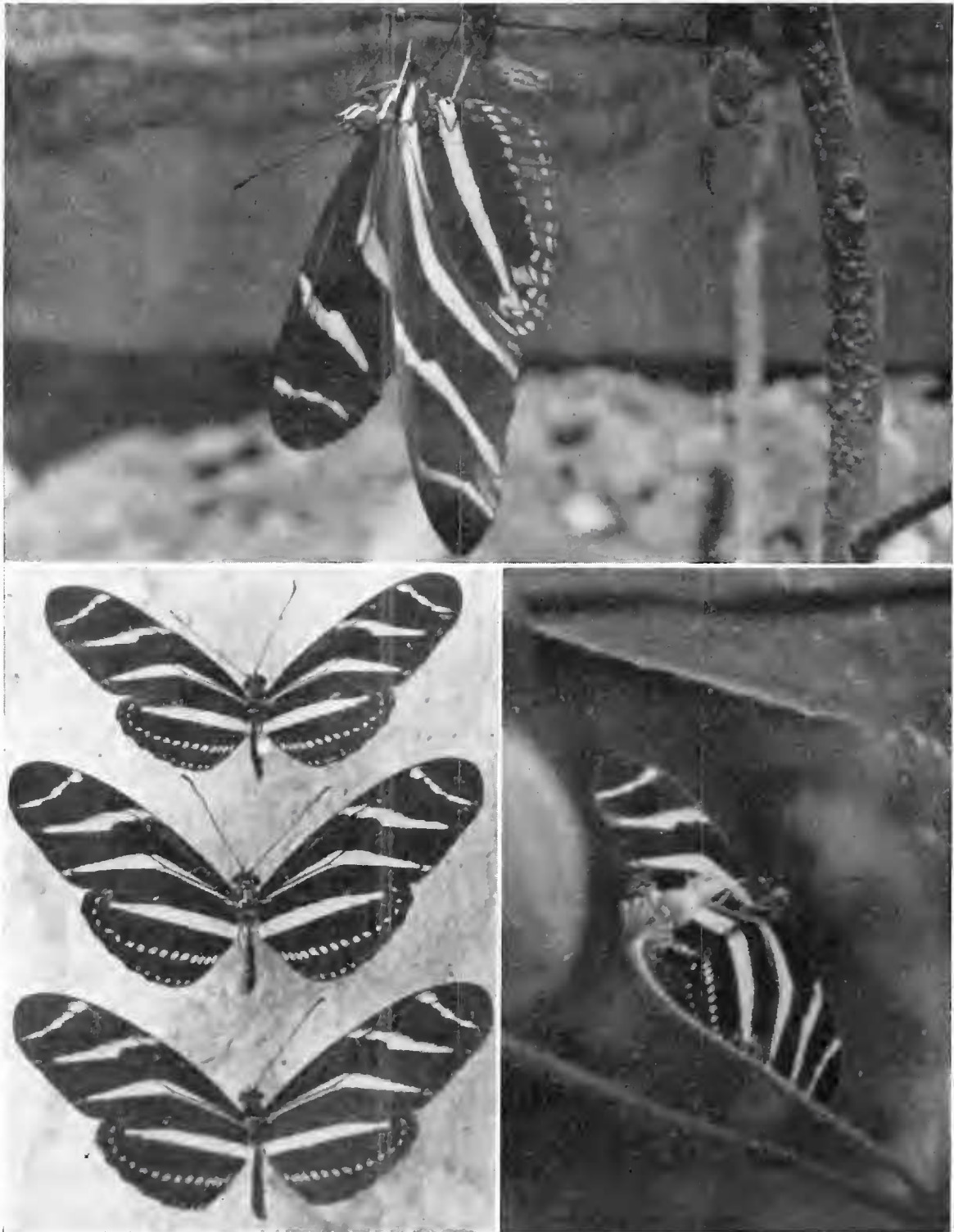


FIG. 4. Adult *Heliconius charitonius*. Upper: an adult female just after eclosion (part of pupa case visible to the right). Lower left: three adults reared from the egg stage in the laboratory; lower right: a young adult feeding on a curcubitaceous flower (February 13, 1976, near La Virgen).

Pupae as Prey.—I searched the vicinity of one vine of *T. lobata* on January 12 and discovered four pupae that later matched the description of the pupa of *H. charitonius* obtained in the rearing studies. All of these were affixed to plants very close to the vine. Two of the pupae were being attacked by ants (Fig. 3). One pupa was virtually eaten down to the

last abdominal segment at this time, and the other pupa (located about one meter from the first one) was just in the initial stages of being eaten by two different types of ants. I observed this pupa for two subsequent days and eventually all that remained was the last two abdominal segments and cremaster. When first discovered the pupa was being eaten near the head appendages by an ant, *Crematogaster* sp. (Fig. 3), but two days later, when about half the pupa was gone, three individuals of a much larger ant (*Ectatomma* sp.) were also present with the other ants (Fig. 3). Subsequently I discovered three more eaten pupae in the same area, giving a total of five pupae found as ant prey.

In the laboratory, three of the original group of eight individuals being reared died as pupae as prey for cockroaches. These pupae were kept in a small screen cage with pupae of other butterflies (Ithomiidae, Brassolidae), but they were the first ones to be attacked by cockroaches during the night.

DISCUSSION

In terms of phylogenetic considerations (Emsley, 1965), *H. charitonius* is one of the advanced species of the genus, and the morphology of its early stages illustrate close relatedness with other species such as *H. hecale* and *H. cydno*, which occur in the same habitat in northeastern Costa Rica. A good characteristic to separate later instar caterpillars of *H. charitonius* from those of *H. cydno* or *H. hecale* is the relatively shorter head scolus in the former species. Also, the pupa is more highly sculptured in *H. charitonius* than in these other species. Recently, Brown and Benson (1975) have argued for the operation of larval mimicry in microsympatric species of *Heliconius*. Even though the caterpillars of differently closely related species of *Heliconius* might be feeding on different host plants in the same habitat, it is held that larval mimicry can act to reduce predation rates by vertebrates. Thus selection would favor the occurrence of species with similar caterpillars in the same habitats. Given divergence in host plants, to reduce competition for larval food, several closely related advanced species might co-occur to reduce predation on caterpillars. Thus it is not unexpected to find *H. charitonius* occurring with *H. hecale*, *cydno*, *erato*, and *sara*. At least one of these species (*H. hecale*) feeds on *Passiflora vitifolia* here, and it indicates divergence in oviposition and larval feeding from *H. charitonius*. In this region of Costa Rica, there are likely no more than seven species of Passifloraceae that could be exploited by *Heliconius*, so that each species may have a different primary larval host plant (Gilbert, 1975).

The multiple oviposition of several eggs on the same vine (either by

the same or different female) suggests that (1) the larval host plant is viewed by the species as an abundant resource, and (2) this species is not food-limited in the caterpillar stage. Strict resource limitation would be normally expected to provide selection pressure favoring a greater scattering of the eggs. Gilbert (1975), however, points out that vines of *Passiflora* generally occur at low densities. All *Heliconius* butterflies are associated with Passifloraceae. Further field observations are needed to see how egg densities of *Heliconius* correlate with vine size or biomass. For example, *H. charitonius* may lay one or few eggs on smaller vines of *T. lobata* than on larger ones. Benson *et al.* (1975), report *T. lobata* as the host plant of *H. charitonius* in southeastern Costa Rica and Panama; my studies indicate that it is also the host plant in northeastern Costa Rica. Benson *et al.* (1975) also report that *H. charitonius* either scatters several eggs on the meristem of *T. lobata*, or else lay a single egg on the meristem. Despite the occurrence of other Passifloraceae in the habitat (and in the same vine patch), only *T. lobata* is locally used as the larval host plant; this points to specialization by *H. charitonius*, something not unexpected (Gilbert, 1975). Lamas (1974) makes some interesting comments regarding larval host plants of the subspecies *peruvianus* of *H. charitonius* (Comstock and Brown, 1950; Brown and Comstock, 1952): he maintains, that in addition to several species of *Passiflora*, this subspecies, presumed near extinction in Lima, Peru, may exploit other plants as larval host plants.

T. lobata is very likely the host plant for this butterfly in other life zones (Holdridge, 1967) in Costa Rica since Standley (1937) mentions that it also occurs in montane tropical wet forest regions. It is possible that *H. charitonius* uses other Passifloraceae as larval host plants in Costa Rica, but for montane rain forest and premontane wet forests on the eastern slopes of the central Cordillera, the primary host plant is *T. lobata*. However, other passifloraceous host plants of *H. charitonius* are known from Costa Rica (Benson *et al.*, 1975). Although *T. lobata* possesses large tendrils, it is interesting that *H. charitonius* does not lay eggs singly on the tendrils of passifloraceous vines (Young, 1973; 1975). There is divergence in the oviposition habits among advanced heliconiines. Brown (1973) reports that *H. nattereri* in Brazil oviposits on *Tetrastylis ovalis*. Apparently this primitive passifloraceous genus is not exploited as a larval host plant by many heliconians.

Larval host plant specialization (i.e., one primary host plant in a given region), expected for most species of *Heliconius* (Gilbert, 1975), couple with considerable mortality of eggs and caterpillars from preda-

tion (Gilbert, 1975), probably keep the adult populations of individual species at or near the carrying capacity of the environment. Predation by ants on *Heliconius* pupae warrants further study in terms of its impact on populations. The well developed and apparently functional extrafloral nectaries of *T. lobata*, *P. vitifolia* and perhaps other microsympatric Passifloraceae used as larval foods may serve to attract pupa predators such as ants. Gilbert (1975) points out that these glands attract predatory insects such as ants and wasps; Ehrlich and Gilbert (1973) found that eggs of *H. ethilla* are eaten in large numbers by ants in Trinidad. Thus the observed disappearances of eggs seen here might be attributed to predation by ants. The fact that only a few out of several vines had *Heliconius* eggs might be indicative of intense egg predation. It is known that the female pupae of *H. charitonius* release a pheromone which attracts males (Edwards, 1881; Emsley, 1965); it would be interesting to know if such a pheromone attracts potential predators such as ants as well.

As adult longevity of *H. charitonius* is high (Cook, Thomason, and Young, in prep.) and vagility generally low (Young and Thomason, 1975; Young and Carolan, 1976), there is further stress placed on *Heliconius* for local species packing, promoting K-selection as the adaptive strategy. It is generally known that *Heliconius* butterflies are distasteful to vertebrate predators, since presumably cyagenic glycosides and alkaloids from Passifloraceae are retained as "plant poisons" in the insects (Gilbert, 1975). Certainly the vivid yellow and black wing color pattern of *H. charitonius* suggests unpalatable properties. Although K-selection might be the general adaptive strategy for these butterflies, in regions of Central America such as northeastern lowland Costa Rica, where a large spectrum of secondary habitats are available at the present time, there is opportunity for species such as *H. charitonius* to be flexible in the adaptive context.

The above considerations suggest that *H. charitonius* and other members of the genus are not food-limited as caterpillars, owing to a variety of factors primarily (1) availability of a large host plant biomass, (2) specialization by different species on different passifloraceous species in the same region, (3) diversity of oviposition habits by different species (Gilbert, 1975), and (4) high levels of mortality of juvenile stages. The large number of *Heliconius* species and other heliconiines that usually exist in the same region (Gilbert, 1975 mentions 10) warrants further field study directed towards elucidating the mechanisms of co-occurrence. At least for *H. charitonius*, from my preliminary studies, (1) host plant specialization, (2) high selectivity of flower-type visita-

tion, (3) apparent high mortality of early stages (yet to be confirmed), (4) well developed adult population cohesiveness, and (5) micro-sympatry with other heliconiines, with perhaps the existence of larval mimicry, suggests K-selection in secondary tropical habitats. Although very preliminary and limited, the flower visitation observations suggest repeated visits to the same flower patches by *H. charitonius* and other species. Perhaps these butterflies are "traplining" for nectar and pollen. Gilbert (1975) mentions that advanced species such as *H. charitonius* are expected to trapline daily for nectar and pollen sources, and that they also trapline for egg laying sites. These properties contribute to adult population cohesiveness.

ACKNOWLEDGMENTS

This research is a by-product of National Science Foundation Grant GB-33060. I am grateful to Lenore Durkee (Grinnell College) and Luis Poveda (Museo Nacional de Costa Rica) for assistance with the identification of plant species. The full cooperation of Dr. J. Robert Hunter of Compañía Agrícola Myristica, S.A. (CAMSA) with logistic details is greatly appreciated. Dr. Paul Kanno identified the ants.

LITERATURE CITED

- ALEXANDER, A. J. 1961a. A study of the biology and behavior of the caterpillars and emerging butterflies of the subfamily Heliconiinae in Trinidad. West Indies. Part I. Some aspects of larval behavior. *Zoologica* 46:1-24.
- ALEXANDER, A. J. 1961b. A study of the biology and behavior of the caterpillars and emerging butterflies of the subfamily Heliconiinae in Trinidad. West Indies. Part II. Molting, and the behavior of pupae and emerging adults. *Zoologica* 46:105-124.
- BEEBE, W., CRANE, J. AND FLEMING, H. 1960. A comparison of eggs, larvae and pupae in fourteen species of heliconiine butterflies from Trinidad, West Indies. *Zoologica* 45:111-154.
- BENSON, W. W., BROWN, K. S., JR., AND GILBERT, L. E. 1975. Coevolution of plants and herbivores: passion flower butterflies. *Evolution* 29:659-680.
- BROWN, F. M. AND COMSTOCK, W. P. 1952. Some biometrics of *Heliconius charitonius* (Linnaeus) (Lepidoptera, Nymphalidae). *Amer. Mus. Novit.* 1574:1-52.
- BROWN, K. S., JR. 1973. A portfolio of neotropical Lepidopterology. Organizacao Tecnica de Taquigrafia e Gravacoes Editora, Rio de Janeiro. 28 pp.
- BROWN, K. S., JR., AND MIELKE, O. H. H. 1972. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part II. Introduction and general comments, with a supplementary revision of the tribe. *Zoologica* 57:1-40.
- BROWN, K. S., JR. AND BENSON, W. W. 1975. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part VI. Aspects of the biology and ecology of *Heliconius demeter*, with description of four new subspecies. *Bull. Allyn Museum* 26:1-19.

- COMSTOCK, W. P., AND BROWN, F. M. 1950. Geographical variation and subspeciation in *Heliconius charitonius* (Lep.: Nymphalidae). Amer. Mus. Novit. 1467:1-21.
- EDWARDS, W. H. 1881. On certain habits of *Heliconia charitonia* Linn., a species of butterfly found in Florida. Papilio 1:209-215.
- EHRlich, P. R. AND GILBERT, L. E. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. Biotropica 5:69-82.
- EMSLEY, M. G. 1965. Speciation in *Heliconius* (Lep., Nymphalidae): morphology and geographic distribution. Zoologica 50:191-254.
- GILBERT, L. E. 1972. Pollen feeding and reproductive biology of *Heliconius* butterflies. Proc. Nat. Acad. Sci. USA 69:1403-1407.
- GILBERT, L. E. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. pp. 210-240, *In* Coevolution of Animals and Plants, L. E. Gilbert *ed.*, Univ. Texas Press. 246 pp.
- HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica. 35 pp.
- JONES, F. M. 1930. The sleeping Heliconias of Florida. Nat. Hist. 30:635-644.
- LAMAS, G. 1974. Supuesta extincion de una mariposa en Lima, Peru (Lepidoptera, Rhopalocera). Revista Peruana de Entomol. 17:119-120.
- POULTON, E. B. 1931. The gregarious sleeping habits of *Heliconius charitonius* L. Proc. Roy. Entomol. Soc. London 6:4-10.
- STANDLEY, W. 1937. The flora of Costa Rica. 210 pp.
- YOUNG, A. M. 1973. Notes on the biology of the butterfly, *Heliconius cydno* (Lepidoptera: Heliconiinae) in Costa Rica. Wasmann J. Biol. 31:337-350.
- YOUNG, A. M. 1975. Observations on the life cycle of *Heliconius hecale zuleike* (Hewitson) in Costa Rica. Pan-Pacific Entomol. 51:76-85.
- YOUNG, A. M. AND THOMASON, J. H. 1975. Notes on communal roosting of *Heliconius charitonius* (Nymphalidae: Heliconiinae) in Costa Rica. J. Lepid. Soc. 29:243-255.
- YOUNG, A. M. AND CAROLAN, M. E. 1976. Daily instability of communal roosting in the butterfly *Heliconius charitonius* in Costa Rica. J. Kansas Entomol. Soc.: In press.